

Latitudinal Gradients in North American Braconid Wasp Species Richness and Biology

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Abstract.—Latitudinal trends in the numbers of species and genera of all subfamilies of Braconidae in America north of Mexico were examined by compiling lists of published records for states (USA) and provinces (Canada) and grouping these into approximate latitudinal belts. The data obtained agree well with past studies on the species richness of Ichneumonidae in North America (Janzen 1981) with peaks in numbers of taxa occurring in the belt lying approximately between 37° and 42° North. The ratio of idiobiont to koinobiont genera and species increased monotonically with decreasing latitude.

Most insect groups increase in species richness with decreasing latitude (see Stephens 1989). However, there is a body of evidence that the species richness and diversity of some groups of insect parasitoids, whilst increasing towards the tropics, does so at a lesser rate than does the species richness and diversity of herbivorous insects (Owen & Owen 1974; Gauld 1986; Noyes 1989). Whilst there is good evidence that the species richness and perhaps also diversity of some groups of parasitic Hymenoptera, such as the Chalcidoidea, increases towards the tropics (e.g. Hespeneide 1979), for others it has been suggested that species richness may even be greater in temperate than in tropical regions, a trend referred to as anomalous diversity (Owen & Owen 1974; Janzen & Pond 1975; Janzen et al. 1976). However, these conclusions have been challenged on the grounds of sampling methodology (Morrison et al. 1978; Hespeneide 1979), and also because they mostly deal with just one family, the Ichneumonidae, and the generality of these findings has yet to be demonstrated.

Janzen (1981) examined the latitudinal distributions of members of eight subfamilies of Ichneumonidae in North America

using the catalogues of Townes. These catalogues were based on an enormous amount of work and were therefore taken to be relatively geographically unbiased, though the possibility does exist that since Townes himself did much of his collecting around Michigan, the taxonomic coverage of that part of the United States may have been relatively more complete. However, Janzen's approach does overcome some of the difficulties encountered when working on tropical versus temperate comparisons in that sampling and taxonomic effort within the temperate region has been comparatively evenly distributed and more thorough because of the long history of collecting and revisionary work that has been carried out there. Surprisingly, Janzen found that the peak in North American ichneumonid species richness occurs between 38° and 42° North, i.e. species richness was not found to increase consistently with decreasing latitude. The question remained, however, whether this result was more generally applicable to other groups of parasitic Hymenoptera. Indeed there is a growing body of evidence to suggest that different groups of parasitoids show quite different trends in their species richness with respect to latitude (Gauld 1986; Askew 1990).

The present work attempts to carry out for the Braconidae, a similar exercise to Janzen's (1981) ichneumonid study. The Braconidae are generally accepted as being the extant sister group of the Ichneumonidae (Sharkey & Wahl 1992), and collectively, the two families constitute the superfamily Ichneumonoidea. Juillet (1964) obtained data from samples of ichneumonoids caught in a rotary trap at a single site in Canada, which suggested that members of the Ichneumonidae 'prefer', and hence are more diverse in, cooler and more humid habitats than members of the Braconidae. Thus, it might be expected that braconids will, as a whole, be more species rich at lower latitudes than ichneumonids, and therefore might not show the same peak in species richness that Janzen found for Nearctic Ichneumonidae. Thus, as pointed out by Wharton (1993a), the distribution of species richness in the Braconidae ought to make an interesting comparison with the Ichneumonidae.

Catalogues and descriptions of Nearctic Braconidae usually provide data on the state or province from which material has been recorded or described. We therefore divided the states of the USA and the Canadian provinces collectively into 5 groups such that each group occupied a reasonably constant latitudinal zone with minimal latitudinal overlap between groups (Fig. 1). The areas of the five zones are given in Table 2. Whilst it was not possible to completely avoid overlap, the effect of such overlaps will be to reduce rather than enhance the likelihood of detecting latitudinal gradients, and consequently our results will be conservative. The resolution of latitudinal trends in the present study is necessarily somewhat coarser than that obtained by Janzen (1981) as information on distributions is only readily available in the form of state or province records.

The primary sources of distributional data were the catalogues of Shenefelt

(1969, 1970a, b, 1972, 1973a, b, 1974, 1975, 1978), Shenefelt & Marsh (1976) and Marsh (1979). We then attempted to take into account many of the subsequently published taxonomic changes so as to allow for new synonymies, new generic placements, newly described taxa and new distribution records (van Achterberg 1977, 1979, 1983, 1985, 1986, 1987, 1988a, b; Čapek & Achterberg 1992; Deyrup 1981; Haeselbarth & Loan 1985; Huddleston 1976; Johnson 1987; Loan 1979; Loan & Holliday 1979; Marsh 1988, 1989, 1991, 1993; Mason 1975, 1976a, b, 1978, 1979, 1981, 1987, 1991; Quicke & Krufft 1995; Quicke & Sharkey 1985; Riegel 1987; Rieske et al. 1989; Saffer 1982; Sharkey 1985, 1988; Sharkey & Mason 1986; Sharkey & Wharton 1985, 1994; Shaw 1983, 1985, 1992, 1993; Sary & Marsh 1982; Wharton 1977a, b, 1980, 1983, 1986, 1988, 1993b, 1994; Wharton & Quicke 1988; Wharton et al. 1989; Wheeler & Loan 1984; Whitfield 1985, 1988a, b; Whitfield & van Achterberg 1987; Whitfield & Mason 1994; Williams 1985, 1988). In addition, a few unpublished data were included for the following taxa: *Vipio* (Braconinae) (Inayatullah 1992); *Pholetesor* (Microgastrinae) (J. Whitfield, in press); undescribed genus of Euphorinae (S. R. Shaw, pers. comm.). The genus *Celerion* is excluded as its subfamilial status is questionable (Marsh, pers. comm.). No data are included for introduced species.

The treatment of subfamilies largely follows that of Quicke & Achterberg (1990) except that the Hormiini and Meteorini are treated here as separate subfamilies.

No pretence is made that this taxonomic treatment is complete, but it is hoped that it is unbiased and, therefore, that any errors that may have been included and any omissions there may be will not affect the results substantially.

RESULTS AND DISCUSSION

The numbers of genera and species of each subfamily recorded as occurring in



Fig. 1. Map of North America showing boundaries of latitudinal zones employed in the present study.

each of the five latitudinal zones are presented in Tables 1 and 2. The subfamilies are arranged in two groups, the first being idiobionts (Table 1) and the second koinobionts (Table 2). As expected, different subfamilies showed markedly different latitudinal trends, though nearly all showed maximum generic and specific representation in our latitudinal zone IV

which corresponds approximately to the latitudinal range from 37° and 42° North. None of the larger subfamilies was found to be most speciose in zone V. Four of these, the Braconinae, Microgastrinae, Macrocentrinae and Opiinae were most diverse in zone III. Our data for the Alysiniinae, usually considered a more temperate and northern group, suggest that within

Table 1. Distributions of genera and species of braconid subfamilies with respect to latitudinal zones (see Fig. 1). Idiobiont taxa

	Subfamilies						Total
	Rhyssalinae	Histero- merinae	Doryctinae	Braconinae	Exothecinae	Hormiinae	
Genera							
Zone I	0	0	2	3	2	1	8
Zone II	2	1	8	9	3	2	25
Zone III	1	1	16	8	4	4	34
Zone IV	2	1	20	7	3	6	39
Zone V	1	1	28	10	2	8	50
Species							
Zone I	0	0	2	4	3	1	10
Zone II	2	1	35	67	4	3	112
Zone III	5	1	72	108	5	5	196
Zone IV	4	1	111	104	3	12	235
Zone V	1	1	105	86	2	11	206

North America, it is at its richest in the middle latitudes of the U.S.A. (zone IV) as with most other subfamilies.

Table 3 provides a comparison of the relative latitudinal distributions of braconid genera and species according to zone and in terms of taxa per unit area. Additionally, it shows the total numbers of idiobiont and koinobiont taxa and the ratios of numbers of koinobiont to idiobiont taxa in each latitudinal zone. The latter show consistent trends for both genera and species, with the ratio of koinobionts to idiobionts decreasing with decreasing latitude.

It has long been recognised that some subfamilies of Braconidae are most species rich in the temperate region whilst others are tropicentric. For example, the Alysiinae, which are entirely koinobiont endoparasitoids of Diptera, are a principally northern group, and whilst there are many undescribed tropical members of the genus *Asobara*, a group that attacks Drosophilidae, more detailed knowledge of these is not likely to change our concept of the subfamilies overall distribution to a major degree. In contrast, the Agathidinae and Cardiochilinae, two groups of koinobiont endoparasitoids of Lepidoptera larvae, are both most speciose in the tropical region

(Sharkey 1992; Huddleston & Walker 1988), and the latter in particular is rather species poor in temperate latitudes. Some groups are restricted in latitudinal range by the distributions of their hosts. For example, members of the ichneumonid subfamily Ctenopelmatinae, most tryphonine ichneumonids, and the braconid tribes Ichneutini and Proteropini (both usually treated as belonging to the Ichneutinae; see Sharkey & Wharton 1994) are all endoparasitoids of sawflies, and since sawflies are most abundant in temperate regions they are likely to support a higher species richness of parasitoids there.

In the case of the Braconidae, life history strategy, idiobioncy and koinobioncy (Askew & Shaw 1986), is very tightly linked with whether the wasps develop as ecto- or endoparasites respectively (Quicke & Achterberg 1990; Shaw & Huddleston 1991). It is not possible therefore, to discern which of these life history features is most responsible for the observed trends. Further, as biology is usually consistent within subfamilies within the Braconidae (Shaw & Huddleston 1991), any latitudinal trends in the ratios of idiobiont to koinobiont taxa will necessarily involve the differential occurrence or representation of subfamilies.

Table 2. Distributions of genera and species of braconid subfamilies with respect to latitudinal zones (see Fig. 1). Koinobiont subfamilies

	Subfamilies											
	Roagadinae	Gnamptodontinae	Opiinae	Alysinae	Apbidinae	Ichneutinae	Dirrhopininae	Adelinae	Cheloninae	Mendesellinae	Miracinae	Cardiochilinae
Genera												
Zone I	2	1	2	13	6	1	0	0	3	0	0	0
Zone II	4	1	6	26	16	3	0	0	5	0	1	1
Zone III	7	1	7	28	13	3	1	2	5	0	1	1
Zone IV	7	1	6	30	12	4	1	2	5	0	1	1
Zone V	7	2	7	18	13	5	1	2	5	1	1	1
Species												
Zone I	3	2	14	73	10	3	0	0	10	0	0	0
Zone II	14	1	64	77	57	4	0	0	55	0	3	3
Zone III	33	2	147	131	54	6	1	2	77	0	4	10
Zone IV	36	4	111	158	70	6	1	4	98	0	5	26
Zone V	31	5	122	55	34	7	1	2	50	1	5	24

Whilst straightforward taxonomic effects are undoubtedly involved in determining the distributions of some groups, there is a growing evidence that trends in species richness and diversity may be correlated with life history strategy. In particular, idiobionts whose hosts by definition do not develop further following initial parasitization (Askew & Shaw 1986) appear to be more species rich at lower latitudes than parasitoid taxa that display the opposite strategy, the koinobionts.

Hawkins et al. (1992) in an attempt to understand better the latitudinal trends in parasitoid diversity in North America, took a different approach in that they concentrated on parasitoid assemblage size per host rather than on the numbers of species in random field samples. Their data showed that latitudinal trends in species richness are influenced not only by whether the parasitoids display idiobiont or koinobiont life history strategies but also by host feeding niche. In particular, they found that the diversity of parasitoids of exophytic hosts decreased with decreasing latitude but that the diversity of

those attacking endophytic hosts increased.

Several hypotheses have been proposed to account for declines in the species richness of some parasitoid groups with decreasing latitude and for trends in the ratios of idiobionts to koinobionts. These include Gauld et al.'s (1992) "nasty" host hypothesis, resource fragmentation hypotheses (Janzen & Pond 1975; Janzen 1981), interphyletic competition (Eggleton & Gaston 1990), parasitoid predation effects (Gauld 1987), host predation effects (Rathcke & Price 1976), and limited speciation opportunity as a result of supposed low host recruitment potential (Shaw 1994). These are not dealt with in detail here as they are reviewed in detail by Hawkins (1994).

Our data show that overall, the latitudinal variation in species richness in North American Braconidae closely resembles that found by Janzen (1981) for Ichneumonidae, with a peak near the central latitudes of the USA and with a distinct decline in the numbers of species and genera occurring in the southernmost

Table 2. Extended

Subfamilies															
Microgasterinae	Euphorinae	Meteorinae	Neoneurinae	Agathidinae	Orgilinae	Microtypinae	Cenocoeliinae	Homolobinae	Charomantinae	Macrocentrinae	Helconinae	Blacinae	Meteoridaeinae	Sigalphinae	Total
11	6	2	0	2	1	1	0	1	1	1	1	2	0	0	58
22	14	2	2	6	1	1	1	2	1	2	12	2	0	1	131
23	17	2	2	5	1	1	1	2	1	2	13	2	1	1	143
21	16	2	2	7	2	1	1	1	1	2	15	1	0	1	143
10	15	2	2	8	2	1	1	2	1	2	10	2	1	1	123
18	6	7	0	2	7	1	0	1	2	2	2	6	0	0	171
122	61	25	3	25	31	1	4	4	2	25	25	17	0	1	634
182	41	30	9	53	49	1	5	4	1	36	57	14	1	1	961
169	43	32	8	61	55	1	8	3	2	32	70	13	0	1	1025
125	33	24	5	51	34	1	8	6	2	23	58	11	1	1	725

states. We have no evidence that sampling in the southern states has been significantly less intense than in more northerly ones though the possibility cannot be excluded. Further, it should be noted that in all five zones some states and provinces have been collected in much more intensively than others. California, a state that has been extensively collected, was in-

cluded in our Zone IV, though it could equally justifiably have been included in Zone V as it straddles the boundary latitude more or less evenly. Reanalysis of the data set with California transferred to Zone V does not reduce the peaks in species and generic richness in zone IV to any great extent.

Extrapolation of the observed trend in

Table 3. Summary of latitudinal distributions of genera and species of Braconidae in North America and ratios of koinobiont to idiobiont taxa

	Total no. of taxa	Area (10 ⁶ km ²)	Total taxa per 10 ⁶ km ²	No. of idiobiont taxa	No. of koinobiont taxa	Koinobiont/Idiobiont
Genera						
Zone I	66	5.19	12.3	8	58	7.25
Zone II	156	5.76	26.9	25	131	5.20
Zone III	177	2.62	66.9	34	143	4.17
Zone IV	182	2.57	70.0	39	143	3.64
Zone V	172	2.63	63.8	50	122	2.42
Species						
Zone I	181	5.19	34.1	10	171	17.10
Zone II	746	5.76	127.4	112	634	5.66
Zone III	1157	2.62	437.4	196	961	4.90
Zone IV	1260	2.57	486.8	235	1025	4.36
Zone V	930	2.63	351.3	206	724	3.51

species richness in North America to more general, temperate/tropical species richness and diversity questions would be unwise. One reason for caution in this respect is that a substantial part of the southern U.S.A. and northern Mexico is markedly arid, and this may restrict parasitoid species richness as it appears to do in North Africa (unpubl. data). Further, even in areas of higher annual rainfall, ichneumonoids may still be limited by water availability since it has been proposed that many may need to drink on a daily basis and rains are typically less regular (Townes 1971). Townes suggested that dew formation may be equally if not more important than rainfall per se in regulating numbers and species richness of ichneumonoids in warmer climates, and that it is for this reason that altitude is an important factor in determining ichneumonoid species richness in the tropics, dew forming more regularly with increasing altitude. In the case of the Southern U.S.A., much of the less arid south is at low altitude and therefore may experience dew less regularly than required by many species of parasitoids. However, interpretation of dew and rainfall data is likely to be far from a simple matter of examining the mean annual number of dew days for particular states, and if water availability is an important factor in limiting ichneumonoid species richness in the more southern states, then rainfall, season, temperature and dew frequency are likely to be involved together in a complex interaction. Further, other important sources of water for many insects of arid region are nectar and honeydew, and availability of these, and their utilization by ichneumonoids, may also need to be considered.

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LITERATURE CITED

- Achterberg, C. van. 1977. A new Holarctic genus, *Spathicopsis* gen. nov., belonging to the Euphorinae, Centistini (Hym., Braconidae). *Entomologische Berichten* 37: 27–31.
- Achterberg, C. van. 1979. A revision of the subfamily Zelinae Auct. (Hymenoptera: Braconidae). *Tijdschrift voor Entomologie* 122: 241–479.
- Achterberg, C. van. 1983. Revisionary notes on the genera *Dapsilarthra* Auct. and *Mesocrina* Foerster (Hymenoptera: Braconidae: Alysiinae). *Tijdschrift voor Entomologie* 126: 1–23.
- Achterberg, C. van. 1985. Notes on Braconidae VI: The genera and subgenera of Centistini, with the description of two new taxa from the Nearctic region (Hymenoptera: Braconidae: Euphorinae). *Zoologische Mededelingen* 59: 348–362.
- Achterberg, C. van. 1986. The holarctic genus *Anisocoryta* Foerster (Hymenoptera: Braconidae: Alysiinae). *Zoologische Mededelingen* 60: 285–297.
- Achterberg, C. van. 1987. Revisionary notes on the subfamily Orgilinae (Hymenoptera: Braconidae). *Zoologische Verhandelingen* 242: 3–111.
- Achterberg, C. van. 1988a. The genera of the *Aspilota*-group and some descriptions of fungicolous Alysiini from the Netherlands (Hymenoptera: Braconidae: Alysiinae). *Zoologische Verhandelingen* 247: 1–88.
- Achterberg, C. van. 1988b. Revision of the subfamily Blacinae Foerster (Hymenoptera: Braconidae). *Zoologische Verhandelingen* 249: 1–324.
- Askew, R. R. 1990. Species diversity of hymenopteran taxa in Sulawesi. Pages 255–260. in W. J. Knight & J. D. Holloway eds *Insects and the Rain Forests of South East Asia (Wallacea)*. Royal Entomological Society, London.
- Askew, R. R. and M. R. Shaw. 1986. Parasitoid communities: their size, structure and development. Pages 225–264. in J. Waage and D. Greathead (eds) *Insect Parasitoids*. London.
- Čapek, M. and C. van Achterberg. 1992. A revision of the genus *Microtypus* Ratzeburg (Hymenoptera: Braconidae). *Zoologische Mededelingen* 66: 323–338.
- Deyrup, M. 1981. A new species of *Cryptoxilos* (Hymenoptera: Braconidae) attacking adult *Lymantria decipens* Leconte (Coleoptera: Scolytidae). *Entomological News* 92: 177–180.
- Eggleton, P. and K. J. Gaston. 1990. "Parasitoid" species and assemblages: convenient definitions or misleading compromises? *Oikos* 59: 417–421.
- Gaston, K. J. and I. D. Gauld. 1993. How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *Journal of Tropical Ecology* 9: 491–499.
- Gauld, I.D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* 11: 155–161.

- Gauld, I. D. 1987. Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society* 30: 299–312.
- Gauld, I. D., K. J. Gaston and D. Janzen. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the “nasty” host hypothesis. *Oikos* 65: 353–357.
- Haeselbarth, E. and C. Loan. 1983. *Townesilitus*, a new genus for a species group in Microctonus (Hymenoptera: Braconidae, Euphorinae). *Contributions of the American Entomological Institute* 20: 384–387.
- Hawkins, B. A. 1994. *Pattern and Process in Host-Parasitoid Interactions*. Cambridge University Press, Cambridge. 190pp.
- Hawkins, B.A. 1990. Global patterns of parasitoid assemblage size. *Journal of Animal Ecology* 59: 57–72.
- Hawkins, B.A., M.R. Shaw and R.R. Askew. 1992. Relations among assemblage size, host specialization and climate variability in North American parasitoid communities. *American Naturalist* 139: 58–79.
- Hespenheide, H.A. 1979. Are there fewer parasitoids in the tropics? *American Naturalist* 113: 766–769.
- Huddleston, T. 1976. A revision of *Elasmosoma* Ruthe (Hymenoptera: Braconidae) with two new species from Mongolia. *Annales Historico-Naturales Musei Nationalis Hungarici* 68: 215–225.
- Huddleston, T. and A. K. Walker. 1988. *Cardiochiles* (Hymenoptera: Braconinae), a parasitoid of lepidopterous larvae, in the Sahel of Africa, with a review of the biology and host relationships of the genus. *Bulletin of Entomological Research* 78: 435–461.
- Inayatullah, M. 1992. A systematic study of the genus *Vipio* Latreille (Hymenoptera: Braconidae) of the Nearctic and Neotropical Regions. Unpublished Ph.D. thesis, University of Wyoming, Laramie.
- Janzen, D.H. 1981. The peak in North American ichneumonid species richness lies between 38° and 42°N. *Ecology* 62: 532–537.
- Janzen, D. H., I. M. Ataroff, M. Farinas, S. Reyes, N. Rincon, A. Soler, P. Soriano and M. Vera. 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8:193–203.
- Janzen, D.H. and C.M. Pond. 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England and Costa Rica. *Transactions of the Royal Entomological Society of London* 127: 33–50.
- Johnson, J. W. 1987. A revision of the species of *Praon* Haliday in North America north of Mexico (Hymenoptera: Aphidiidae). *Canadian Entomologist* 119: 999–1025.
- Juillet, J. A. 1964. Influence of weather on flight activity of parasitic Hymenoptera. *Canadian Journal of Zoology* 42: 1133–1141.
- Loan, C.C. 1979. Three new species of *Peristenus* Foerster from Canada and Western Europe (Hymenoptera: Braconidae: Euphorinae). *Naturaliste Canadienne* 106: 387–391.
- Loan, C.C. and N.J. Holliday. 1979. Euphorinae parasitic on ground beetles with descriptions of *Microctonus* Wesmael (Hymenoptera: Braconidae, and Coleoptera: Carabidae). *Naturaliste Canadienne* 106: 393–397.
- Marsh, P. M. 1979. Family Braconidae. Pages 144–293. in K. V. Krombein et al. eds *Catalogue of the Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington D. C.
- Marsh, P.M. 1988. Revision of the tribe Odontobraconini in the western hemisphere (Hymenoptera: Braconidae: Doryctinae). *Systematic Entomology* 13: 443–464.
- Marsh, P. M. 1989. Notes on Braconidae (Hymenoptera) associated with Jojoba (*Simmondsia chinensis*) and descriptions of new species. *Pan-Pacific Entomologist* 65: 58–67.
- Marsh, P. M. 1991. A new species of *Pauesia* (Hymenoptera: Braconidae, Aphidiinae) from Georgia and introduced into South Africa against the black pine aphid (Homoptera: Aphididae). *Journal of Entomological Science* 26:81–84.
- Marsh, P. M. 1993. Descriptions of new western hemisphere genera of the subfamily Doryctinae (Hymenoptera: Braconidae). *Contributions of the American Entomological Institute* 28: 1–58.
- Mason, W.R.M. 1975. A new Nearctic *Apanteles* (Hymenoptera: Braconidae) from Oregon grape (Berberidaceae). *Canadian Entomologist* 107: 1133–1135.
- Mason, W.R.M. 1976a. A revision of *Dyscoletes* Haliday (Hymenoptera: Braconidae). *Canadian Entomologist* 108: 855–858.
- Mason, W.R.M. 1976b. The identity of *Macrocentrus uniformis* Provancher (nec Cresson), description of a sibling species and a possible grooming organ (Hym.: Braconidae). *Naturaliste Canadienne* 103: 513–515.
- Mason, W.R.M. 1978. A synopsis of the Nearctic Braconini, with revisions of Nearctic species of *Ceoloides* and *Myosoma* (Hymenoptera: Braconidae). *Canadian Entomologist* 110: 721–768.
- Mason, W. R. M. 1979. A new *Rogas* (Hymenoptera: Braconinae) parasite of tent caterpillars (*Malacosoma* spp. Lepidoptera: Lasiocampidae) in Canada. *Canadian Entomologist* 111: 783–786.
- Mason, W.R.M. 1981. The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): A phylogeny and reclassification of Microgasterinae. *Memoirs of the Entomological Society of Canada* 115: 1–147.
- Mason, W.R.M. 1987. *Vadium*, a new genus of Nearc-

- tic Braconidae (Hymenoptera). *Proceedings of the Entomological Society of Washington* 89: 325–328.
- Mason, W.R.M. 1991. A new genus of exodont Ichneutinae (Hymenoptera: Braconidae). *Insecta Mundi* 5: 95–99.
- Morrison, G., M. Auerbach and E.D. McCoy. 1978. Anomalous diversity of tropical parasitoids: A general phenomenon? *American Naturalist* 114: 303–307.
- Noyes, J.S. 1989. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecological Entomology* 14: 197–207.
- Owen, D.F. and J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249: 583–584.
- Quicke, D.L.J. and Achterberg, C. van. 1990. Phylogeny of the subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandlungen* 258: 1–95.
- Quicke, D. L. J. and R. A. Kruft. 1995. Species of *Yelicones* (Hymenoptera: Braconidae: Rogadinae) in North America with descriptions of two new species. *Annals of the Entomological Society of America* 88: 129–138.
- Quicke, D.L.J. and M.J. Sharkey. 1989. A key to and notes on the genera of Braconinae (Hymenoptera: Braconidae) from America north of Mexico with descriptions of two new genera and three new species. *Canadian Entomologist* 121: 337–361.
- Rathcke, B.J. and P.W. Price. 1976. Anomalous diversity of tropical ichneumonid parasitoids: a predation hypothesis. *American Naturalist* 110: 889–893.
- Riegel, 1982. The American species of Dacninae, excluding certain Dacnusiini (Hymenoptera: Braconinae). *Novitates Arthropodae* 1(13): 1–185.
- Rieske, L. K., D. W. A. Hunt and K. F. Raffa. 1989. *Microctonus pachylobii* (Hymenoptera: Braconidae) parasitizes *Hylobius* weevils in Wisconsin: New host genus and geographic records. *Entomological News* 100: 153–154.
- Saffer, B. 1982. A systematic revision of the genus *Cenocoelius* (Hymenoptera: Braconidae) in North America including Mexico. *Poliskie Pismo Entomologiczne—Bulletin Entomologique de Pologne* 52: 73–167.
- Sharkey, M. J. 1985. Notes on the genera *Bassus* Fabricius and *Agathis* Latreille, with a description of *Bassus arthurellus* n. sp. (Hymenoptera: Braconinae). *Canadian Entomologist* 117: 1497–1502.
- Sharkey, M. J. 1988. A taxonomic revision of *Alabargus* (Hymenoptera: Braconinae). *Bulletin of the British Museum (Natural History) Entomology*, 57: 311–437.
- Sharkey, M. J. 1992. Cladistics and tribal classification of the Agathidinae (Hymenoptera: Braconinae). *Journal of Natural History* 26: 425–447.
- Sharkey, M. J. and W. R. M. Mason. 1986. The generic validity of *Aenigmostonus* and *Asiacardi-ochiles* (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 88: 300–302.
- Sharkey, M. J. and D. Wahl. 1992. Cladistics of the Ichneumonoidea (Hymenoptera). *Journal of Hymenoptera Research* 1: 15–24.
- Sharkey, M. J. and R. A. Wharton. 1985. Redefinition of *Megagathis* Kreichbaumer, and reassignment of New World species to *Zacremnops* new genus (Hymenoptera: Braconinae: Agathidinae). *Canadian Entomologist* 177: 599–603.
- Sharkey, M. J. and R. A. Wharton. 1994. A revision of the genera of the world Ichneutinae (Hymenoptera: Braconidae). *Journal of Natural History* 28: 873–912.
- Shaw, M. R. 1994. Parasitoid host ranges. in B. A. Hawkins and W. Sheehan eds *Parasitoid Community Ecology*. Oxford University Press. pp. 111–144.
- Shaw, M. R. and T. Huddleston. 1991. Classification and biology of braconid wasps. *Handbooks for the Identification of British Insects* 7: 1–126.
- Shaw, S.R. 1983. A taxonomic study of Nearctic *Ascogaster* and a description of a new genus *Leptodrepana* (Hymenoptera: Braconidae). *Entomography* 2: 1–54.
- Shaw, S.R. 1985. A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). *Entomography* 3: 277–370.
- Shaw, S.R. 1992. Seven new North American species of *Neoneurus* (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 94: 26–47.
- Shaw, S. R. 1993. Systematic status of *Eucystomastax* Brues and characterization of the Neotropical species (Hymenoptera: Braconidae: Rogadinae). *Journal of Hymenoptera Research* 2: 1–11.
- Shenefelt, R. D. 1969. *Hymenopterorum Catalogus* (nova editio), Pars 4, Braconidae 1. Hybrizoninae, Euphorinae, Cosmophorinae, Neoneurinae, Macrocentrinae. The Hague, Junk. 176 pp.
- Shenefelt, R. D. 1970a. *Hymenopterorum Catalogus* (nova editio), Pars 5, Braconidae 2. Helconinae, Calyptinae, Mimagathidinae, Triaspininae. The Hague, Junk. 130 pp.
- Shenefelt, R. D. 1970b. *Hymenopterorum Catalogus* (nova editio), Pars 6, Braconidae 3. Agathidinae. The Hague, Junk. 124 pp.
- Shenefelt, R. D. 1971. *Hymenopterorum Catalogus* (nova editio), Pars 7, Braconidae 4. Microgasterinae, Apanteles. The Hague, Junk. 243 pp.
- Shenefelt, R. D. 1973a. *Hymenopterorum Catalogus* (nova editio), Pars 9, Braconidae 5. Microgasterinae & Ichneutinae. The Hague, Junk. 144 pp.
- Shenefelt, R. D. 1973b. *Hymenopterorum Catalogus* (nova editio), Pars 10, Braconidae 6. Cheloninae. The Hague, Junk. 124 pp.

- Shenefelt, R. D. 1974. *Hymenopterorum Catalogus* (nova editio), Pars 11, Braconidae 7. Alysiinae. The Hague, Junk. 180 pp.
- Shenefelt, R. D. 1975. *Hymenopterorum Catalogus* (nova editio), Pars 12, Braconidae 8. Exothecinae, Rogadinae. The Hague, Junk. 150 pp.
- Shenefelt, R. D. 1978. *Hymenopterorum Catalogus* (nova editio). Part 15. Braconidae, vol. 10. Braconinae, Gnathobraconinae, Mesostoinae, Pseudodicrogeniinae, Telengainae, Ypsistocerinae plus Braconidae in general, major groups, unplaced genera and species. The Hague, Junk, 440 pp.
- Shenefelt, R. D. and P. M. Marsh. 1976. *Hymenopterorum Catalogus* (nova editio), Pars 13, Braconidae 9. Doryctinae. The Hague, Junk. 162 pp.
- Stary, P. and P. M. Marsh. 1982. A new species of *Trioxys* (Hymenoptera: Aphidiidae) parasitic on a pecan aphid. *Proceedings of the Entomological Society of Washington* 84: 726–728.
- Stephens, G. S. 1989. The latitudinal gradient in geographic range: How so many species coexist in the tropics. *American Naturalist* 133: 240–256.
- Townes, H. 1971. Ichneumonids as biological control agents. *Proceedings of the Tall Timbers Conference on Ecological Animal Control by Habitat Management*. pp. 235–248.
- Wharton, R. A. 1977a. New World *Aphaereta* species (Hymenoptera: Braconidae: Alysiinae), with a discussion of terminology used in the tribe Alysiini. *Annals of the Entomological Society of America* 70: 782–803.
- Wharton, R. A. 1977b. Exodontiellini, a new tribe of Opiinae with exodont mandibles (Hymenoptera: Braconidae). *Pan-Pacific Entomologist* 53: 297–303.
- Wharton, R.A. 1980. Review of the Nearctic Alysiini (Hymenoptera: Braconidae) with discussion of the generic relationships within the tribe. *Entomology* 88: 1–112.
- Wharton, R.A. 1983. New species of *Illidops* and *Bracon* (Hymenoptera: Braconidae) of potential use in biological control. *Canadian Entomologist* 115: 667–672.
- Wharton, R.A. 1986. The braconid genus *Alysia* (Hymenoptera): a description of the subgenera and a revision of the subgenus *Alysia*. *Systematic Entomology* 11: 453–504.
- Wharton, R.A. 1988. The braconid genus *Alysia* (Hymenoptera): A revision of the subgenus *Anarcha*. *Contributions of the American Entomological Institute* 25: 1–69.
- Wharton, R. A. 1993a. Bionomics of the Braconidae. *Annual Review of Entomology* 38: 121–143.
- Wharton, R. A. 1993b. Review of the Hormiini (Hymenoptera: Braconidae) with a description of new taxa. *Journal of Natural History* 27: 107–171.
- Wharton, R. A. 1994. New genera, species and records of New World Alysiinae (Hymenoptera: Braconidae). *Proceedings of the Entomological Society of Washington* 96: 630–664.
- Wharton, R.A., and D.L.J. Quicke. 1988. A new species of *Bracon* (Hymenoptera: Braconidae) parasitic on *Eoreuma loftini* (Dyar) (Lepidoptera: Pyralidae). *Proceedings of the Entomological Society of Washington* 90: 288–293.
- Wharton, R.A., J. W. Jr. Smith, D.L.J. Quicke and H. W. Browning. 1989. Two new species of *Digonogastra* Viereck (Hymenoptera: Braconidae) parasitic on Neotropical pyralid borers (Lepidoptera) in maize, sorghum and sugarcane. *Bulletin of Entomological Research* 79: 401–410.
- Wheeler, A. G. Jr, and C. C. Loan, 1984. *Peristenus henryi* (Hymenoptera: Braconidae, Euphorinae) a new species parasitic on the honeylocust plant bug, *Diaphnocoris chlorionis* (Hemiptera: Miridae). *Proceedings of the Entomological Society of Washington* 86: 669–672.
- Whitfield, J.B. 1985. The Nearctic species of *Deuterixys* Mason (Hymenoptera: Braconidae). *Pan-Pacific Entomologist* 61: 60–67.
- Whitfield, J.B. 1988a. Revision of the Neactic species of the genus *Stiropius* Cameron (= *Bucculatrixplex* Auct.) with the description of a new related genus (Hymenoptera: Braconidae). *Systematic Entomology* 13: 373–385.
- Whitfield, J.B. 1988b. Two new species of *Paradelius* (Hymenoptera: Braconidae) from North America with biological notes. *Pan-Pacific Entomologist* 64: 313–319.
- Whitfield, J.B. and C. van Achterberg. 1987. Clarification of the taxonomic status of the genera *Cantharoctonus* Viereck, *Noserius* Foerster and *Pseudavga* Tobias (Hymenoptera: Braconidae). *Systematic Entomology* 12: 509–518.
- Whitfield, J. B. and W. R. M. Mason. 1994. Mendsellinae, a new subfamily of braconid wasps (Hymenoptera, Braconidae) with a review of relationships within the microgastroid assemblage. *Systematic Entomology* 19: 61–76.
- Williams, D. J. M. 1985. The New World genus *Lathrapanteles* n. gen.: Phylogeny and placement in Microgastrinae (Hymenoptera: Braconinae: Cotesiini). *Canadian Journal of Zoology* 63: 1962–1981.
- Williams, D. J. M. 1988. Classification, phylogeny and zoogeographic studies of species of *Sathon* Mason (Hymenoptera: Braconidae). *Quaestiones Entomologicae* 24: 529–639.
- Williamson, M. 1988. Relationship of species number to area, distance and other variables. Pages 91–115. in A.A. Myers and P.S. Giller eds *Analytical Biogeography*. Chapman and Hall, London.